Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

A BIMODAL VARIATION POLYGON IN SYNDESMON THALICTROIDES AND ITS MORPHOLOGIL SIGNIFICANCE

DR. J. ARTHUR HARRIS

Carnegie Institution of Washington

In the spring of 1906 I had occasion to count the number of leaf laminæ in the involucres of a series of four hundred inflorescences of *Syndesmon thalictroides* collected from the north slope of a hill at Meramec Highlands, Missouri. In making the records, each distinct lamina was counted, whether it was leaf or leaflet, the immediate purpose of the work being to get some idea of the variability in the number of divisions of the leaf surface in the involucral whorl and the degree of interdependence of the number of laminæ and the number of flowers for comparison with studies already made of the correlation between length of stalk and number of flowers per umbel in Nothoscordium and Allium,[1] and between number of flowers per inflorescence and number of ovules or seeds per ovary in Cercis[2] and Celastrus.[3] When I gathered the material I was quite aware that this rough method of lumping the laminæ is not suited to bring out the morphological significance of the data, but only a little time was available for the work and for the purpose then in hand the method of treatment seemed quite adequate.

These data are shown in the form of a correlation surface in Table I.

It is quite unnecessary to publish graphs for these two distributions to show the conspicuously bimodal character. For the number of laminæ, there are conspicuous modes on 4 and 6, and for the number of flowers, pronounced modes on 1 and 3.

---

[1] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

[2] Harris, J. Arthur, *Biometrika*. In press.

[3] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

Bimodal and multimodal polygons have received so much attention in the literature of variation that the interest of a more detailed investigation was at once apparent. Before considering further our data on this species we may note the more important discussion of these anomalous frequency distributions.

TABLE I

Total Laminæ and Total Flowers per Inflorescence

Flowers per Inflorescence

		1	2	3	4	Totals.
Laminæ per Inflorescence.	1	1	—	—	—	1
	2	1	—	—	—	1
	3	4	1	1	—	6
	4	38	25	47	—	110
	5	9	18	28	—	55
	6	36	22	158	2	218
	7	1	1	2	4	8
	8	—	—	—	1	1
Totals.		90	69	236	7	400

Bateson[4] gives a bimodal variation polygon for the length of horns in the beetle *Xylotrupes gideon* and the length of the forceps in the earwig, *Forficula auricularia*, but the factors underlying the phenomena are not demonstrated. Naturally the first suggestion concerning a bimodal or polymodal polygon is that there is taxonomic heterogeneity in the material examined. Davenport and Blankenship[5] have even suggested criteria for determining whether the component elements of a two-humped curve are to be designated as "varieties" or "species." So far as I am aware the first attempt to analyze a bimodal polygon into its component elements is that of De Vries[6] with *Chrysanthemum segetum*. Pearson[7] in the first of his "Mathematical Contributions to the Theory of Evolution" deals with the mathematical analysis of composite frequency curves.

---

[4] Bateson, W., "Materials for the Study of Variation," pp. 37–42, fig. 2–3, 1894.

[5] Davenport, C. B., and J. W. Blankinship, *Science*, N. S., Vol. VII, pp. 685–694, 1898.

[6] De Vries, H., *Archiv für Entwickelungsemechanik*, Vol. II, 1895; also *Ber. Deutsch. Bot. Ges.*, Vol. XVII, pp. 84–98, 1899; also "Die Mutationstheorie," Vol. I, pp. 526–529; Vol. II, p. 349.

Dimorphism referable to peculiar environmental conditions has received considerable attention, but unfortunately quantitative data are not numerous. For seasonal dimorphism in Idotheca, Gadzikiewicz[8] has published some figures which yield very different polygons for the body length of September and March females.

The above cases are illustrative merely and make no pretense at completely setting forth the literature.

Ludwig and his pupils have devoted a whole series of papers[9] to the discussion of multimodal variation polygons. De Vries in "Die Mutationstheorie" lays considerable stress upon the Fibonacci series. More recently Ritter[10] and Heyer[11] have taken up the questions and the reader should consult these papers for a full statement of the problems and the pertinent literature. In any discussions in this field, the warnings set forth in papers by Pearson[12] and by Pearson, Yule, Tower and Lee[13] on the sources of apparent polymorphism in plants should always be kept clearly in mind.

Here I do not care to discuss the work of those who conclude that frequency curves have modes where they would be expected in accordance with some mathematical series. It is obvious to any one trained in working with numbers that there are serious difficulties in the way of demonstrating a number of modes in a frequency distribution. The errors of random sampling can not be disregarded and when the variation is continuous instead of discrete the chances of errors due to biased judgment are great. These facts emphasize the necessity for seeking out the simplest possible cases of polymorphism and determining in so far as possible the morphological conditions which underlie them. Such a case seems to be offered by the involucral leaves of Syndesmon.

---

[7] Pearson, K., *Phil. Trans. Roy. Soc. Lond.*, A., Vol. CLXXXV, pp. 71–110.

[8] Gadzikiewicz, *Bull. Acad. Sci. St. Petersb.*, Vol. XXIV, pp. 263–272, 1906; also *Biolog. Centralbl.*, Vol. XXVII, pp. 505–508, 1907.

[9] A complete bibliography of this work is quite out of place here. The reader may consult F. Ludwig, *Biometrika*, Vol. I, pp. 11–29, 1901, for a general statement of some of Ludwig's own views. See also citations by Ritter.

[10] Ritter, G., *Beih. Bot. Centralbl.*, Abth. II, Vol. XXII, pp. 317–330, 1907; Abth. I, Vol. XXIII, pp. 273–319, 1908; Abth. I, Vol. XXV, pp. 1–29, 1909. Rather full citations of the literature are given in these papers.

[11] Heyer, A., *Biometrika*, Vol. VI, pp. 354–365, 1909.

[12] Pearson, K., *Biometrika*, Vol. I, pp. 260–261, 1902.

[13] Pearson, K., G. U. Yule, W. Tower and A. Lee, *Biometrika*, Vol. I, pp. 304–319, 1902. See also a note on a paper by Shull, *Biometrika*, Vol. II, pp. 113–114, 1902.

After I had made my first series of countings a paper by Kellerman[14] giving the essential morphological features of the leaves and considerable statistical data concerning their variation came to my notice. He does not present his data in a form suitable for statistical consideration, and did not note the bimodal condition which appears where a curve is plotted for the entire number of laminæ.

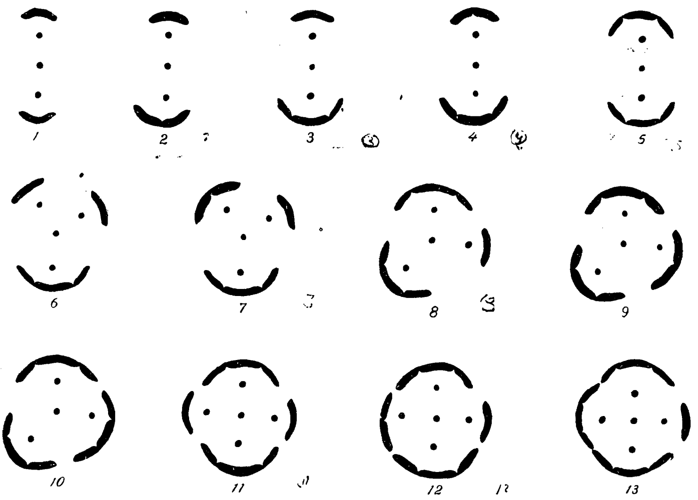
Kellerman's diagrams represent the morphology of the inflorescence very well and are reproduced here with such additional ones as are necessary to represent the types of leaves observed in our series. The terminal and axillary buds which may develop into flower-bearing axes are represented by solid dots. The number of leaflets into which a leaf is divided is indicated by the partial division of the line representing the leaf. Unfortunately Kellerman's data are rather too few to be given further statistical analysis. For figures illustrating the general appearance of different inflorescences the reader may consult his plate.

Most simply the inflorescence consists of a terminal flower, two involucral leaves and two axillary flowers. The axillary buds do not always develop. The leaves may be entire or divided into (generally) three leaflets.

The form of inflorescences with two leaves, one terminal flower and two axillary flowers is shown in Figs. 1 to 5. In our series we find all cases from those with both leaves simple to those with both leaves ternately compound.

---

[14] Kellerman, W. A., *Ohio Nat.*, Vol. I, pp. 107–110, 1901.



Inflorescences of Seq.

In the next group of inflorescences an extra leaf is added. The additional axillary bud thus introduced raises the normal number of pedicels to four. Among the inflorescences with a whorl of three leaves I found none in which at least one of the leaves was not ternately com-

TABLE II

FREQUENCY OF DIFFERENT TYPES OF INFLORESCENCES WITH 2 LEAVES

Class.	f	Class.	f
1—1—**3** (3)	1	3—2—**3** (3)	13
1—1—**3** (2)	0	3—2—**3** (2)	7
1—1—**3** (1)	1	3—2—**3** (1)	11
Fig. 1		Fig. 4	
2—1—**3** (3	0	3—3—**3** (3)[15]	297
2—1—**3** (2)	2	3—3—**3** (2)	95
2—1—**3** (1)	1	3—3—**3** (1)	74
Fig. 2		Fig. 5	
3—1—**3** (3)	9		
3—1—**3** (2)	16	Total.	544
3—1—**3** (1)	17		
Fig. 3			

pound, but in three of them two of the leaves were simple. The different normal types observed are made clear by diagrams 6 to 10.

TABLE III

Frequency of Different Types of Inflorescences with 3 and 4 Leaves

Class.	*f*	Class.	
3—1—1—**4** (4)	2	3—3—2—**4** (5)[18]	1
3—1—1—**4** (3)	1	3—3—2—**4** (4)	4
3—1—1—**4** (2)	0	3—3—2—**4** (3)	0
3—1—1—**4** (1)	0	3—3—2—**4** (2)	1
Fig. 6		3—3—2—**4** (1)	0
3—2—1—**4** (4)	1	Fig. 9	
3—2—1—**4** (3)	0	3—3—3—**4** (4)	6
3—2—1—**4** (2)	0	3—3—3—**4** (3)	2
3—2—1—**4** (1)	1	3—3—3—**4** (2)	0
Fig. 7		3—3—3—**4** (1)	0
3—3—1—**4** (5)[16]	3	Fig. 10	
3—3—1—**4** (4)[17]	76	Total.	137
3—3—1—**4** (3)	15	3—3—1—1—**5** (5)	1
3—3—1—**4** (2)	7	3—3—1—1—**5** (3)	1
3—3—1—**4** (1)	17	Fig. 11	
Fig. 8		3—3—2—1—**5** (5)	1
		Fig. 12.	
		3—3—3—1—**5** (3)	1
		Fig. 13	
		Total.	4

Finally, four leaves with the possibility of four axillary pedicels may be found. The condition of the division of these leaves into leaflets is shown in Figs. 11 to 13.

---

[15] We may note four slightly abnormal inflorescences of the 3—3—**3** type. In one there was concrescence of the terminal and one axillary pedicel for some distance from the base. In another one of the axillary peduncles bore a lateral leaf. In a third the central of the three leaflets of one of the leaves was again divided into three secondary leaflets. In the fourth case the two leaves were not opposite, as is usually the case, but were considerably separated on the axis.

[16] In one of these three cases two peduncles are produced from one of the axils. In the other two, one of the axillary pedicels bears a leaf subtending a secondary pedicel bearing the fifth fruit.

[17] In one of these 76 cases the fourth flower is due to one of the lateral pedicels bearing a leaf in the axil of which a secondary pedicel is borne; one of the axillary buds produces no flower in this case. In two other cases one of the axillary pedicels bore a leaf, but no pedicel was produced in its axil. In one of these cases one of the three leaflets—a lateral one—was again divided into two secondary leaflets.

[18] The fifth flower is due to two axillary pedicels being produced from one of the leaves.

Certain "teratological" cases are not represented by figures, but are described merely.

We may now turn to the important question of the frequency of the several morphological types in the Cold Spring Harbor collection made in the spring of 1909.

In classifying these inflorescences all which were injured in any way so that the number of primary divisions of the leaf could not be made out with certainty were discarded. Especial care was used in cases in which a leaf was apparently divided into two leaflets, since such often results from the breaking off of one of the lateral leaflets of a ternately compound leaf. In some cases inflorescences were included in which the laminæ of the primary leaflets were not intact, so that the data can not be trusted for the frequency of secondary divisions. In counting, only completely divided laminæ were considered as leaflets.

Petiolate leaves were not infrequently found, but no special record was kept of them.

The data are set forth in minutely analyzed form in Table II–III. The light-faced numbers separated by dashes represent the number of primary leaflets into which the leaves are divided. The black-faced numbers show the number of flower-buds—terminal and axillary—which might normally have developed, and the number immediately following in parentheses shows the number actually developing. The *f* (= frequency) column gives the number of occurrences of each type.

Grouping the data according to the number of leaves per inflorescence, we find:

Two leaves, in	544	cases.
Three leaves, in	137	cases.
Four leaves, in	4	cases.
	685	altogether.

Here is an example of what De Vries[19] has termed a half-Galton curve. Whether it would be possible to increase the number of leaves by selection as De Vries was able to do in the case of the petals of Ranunculus could only be determined by direct experiment. Possibly the skew curve here found is merely due to the age or vigor of the individuals.

---

[19] De Vries, H., *Ber. Deutsch. Bot. Ges.*, Vol. XII, pp. 197–207, 1894.

Considering next the distribution of the number of primary leaflets per leaf in the material we may seriate the number of leaflets for each class of plants separately, as in Table IV.

TABLE IV

Number of Primary Leaflets per Leaf in Leaves from all Different Classes of Inflorescences

Leaves per Inflorescence

		2	3	4	Totals.
Lobes per Leaf.	1	49	126	6	181
	2	34	8	1	43
	3	1005	277	9	1291
Totals.		1088	411	16	1515

Only sixteen leaves were available for the inflorescences producing four leaves, but for those with two and three leaves the number is ample. In each of the three classes of inflorescences, and in the total, there is a pronounced mode on undivided leaves and on those with three leaflets. Throughout, those with two leaflets are much less frequent than those with either one or three.

Reducing the frequencies for the inflorescences with two and three leaves to a percentage basis for more direct comparison, and laying them side by side in Figs. 14 and 15, we note at once that there is a wide difference in the proportion of single leaves in the two series. The source of this difference is at once clear. In the inflorescences with the third leaf, the additional leaf is nearly always simple. Thus the proportion springs at once from about 4.5 per cent. to 30.5 per cent.

Unfortunately, our data, though extensive, are not numerous enough to permit of further analysis. If material were more ample it might be possible to ascertain more precisely some of the factors determining the condition of division of the leaf. All that we can conclude from the present data is that: (*a*) There is a strong tendency to the production of either simple or ternately compound leaves—those divided into two leaflets are rare; (*b*) a larger proportion of the leaves are simple in inflorescences with three or four leaves than in those with but two leaves.

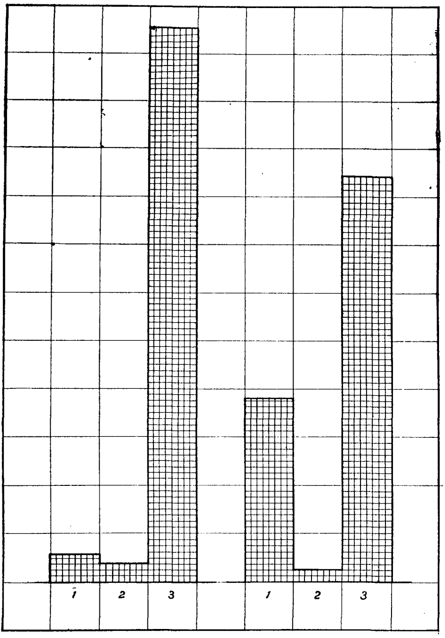


FIG. 14. FIG. 15.

To determine whether the distribution for number of leaf laminæ per involucre in this series forms a bimodal distribution similar to that found in 1905, I extract the totals from the two tables of data. To ascertain more accurately the real source of the bimodal condition, should it be found to exist in this series, the combinations which give rise to the different total numbers are given in Table V.

From these figures appear several points which could not be determined at all on the lumped data as collected in 1905.

The grand total shows that there is a slight empirical mode on four and a conspicuous one on six laminæ, as compared with the very prominent modes on these two grades in 1905. The distributions from the three classes of inflorescences shows the origin of these modes very clearly. The mode on four is due entirely to the tendency to the production of one ternately compound and one simple leaf. Both of these types of leaves have been shown to be much more frequent than those divided into two leaflets. The mode on six is due to both of the involucral leaves bearing the modal (three) number of leaflets.

TABLE V

SHOWING THE FREQUENCY AND MODE OF ORIGIN OF THE DIFFERENT TOTAL NUMBERS OF LAMINÆ PER INFLORESCENCE

Laminæ of Individual Leaves

	Two Leaves.						Three Leaves						Four Leaves.				
Total Laminæ per Inflorescence.	1—1	2—1	3—1	3—2	3—3	Totals.	3—1—1	3—2—1	3—3—1	3—3—2	3—3—3	Totals.	3—3—1—1	3—3—2—1	3—3—3—1	Totals.	Grand Totals.
2	2					2											2
3		3				3											3
4			42			42											42
5				31		31	3					3					34
6					466	466		2				2					468
7									118			118					118
8										6		6	2			2	8
9											8	8		1		1	9
10															1	1	1
	2	3	42	31	466	544	3	2	118	6	8	137	2	1	1	4	685

In the 1905 series inflorescences with seven leaflets formed only 2 per cent. of the population; in the 1909 lot they are over 17 per cent. of the total number. There is no way of determining absolutely why there is such a difference, but it seems quite logical to suppose that in the Cold Spring Harbor series inflorescences with three leaves were much more abundant than in the Meramec Highlands lot, for the frequency of seven laminæ in the Cold Spring Harbor material is entirely due to flowering stalks with three leaves of which two are ternately compound and the third undivided.

In the 1905 series all the laminæ found in the inflorescence were included in the countings. In the discussions just given I have treated only the primary leaflets. The data for the other laminæ are included in the notes on the tables of data or in the notes on teratological cases. Their addition would make little difference in our distributions, but the data are available for any one who cares to use them.

TABLE VI

SERIATION OF NUMBER OF FLOWERS DEVELOPING IN DIFFERENT TYPES OF INFLORESCENCES

Leaves per Inflorescence

Flowers per Inflorescence.	2	3	4	Totals.
1	104	18	—	122
2	120	8	—	128
3	320	18	2	340
4	—	89	—	89
5	—	4	2	6
	544	137	4	685

Further analysis of the data for leaf characters is not justified by the quantity of material. Two conclusions are seen to be amply justified by the facts: (*a*) In Syndesmon there is a strong tendency to the production of simple and trifoliate leaves. (*b*) The preceding fact, taken in connection with the peculiarities of the inflorescence with regard to the number of leaves produced, is quite sufficient to account for the bimodal condition of the variation polygon for number of laminæ per inflorescence.

The bimodal polygon is therefore explicable on purely morphological grounds without any assumption of the mixture of two or more "races" or "minor species," provided the plants producing two, three and four leaves per inflorescence be not considered "small species" or "biotypes." Personally I see no reason whatever to think that they are, but in these days of minute segregation the possibility must not be left unmentioned. To me it seems not unlikely that the three different classes of inflorescences noted are to some extent to be referred to age differences in the individuals producing them.

The number of flowers developing may now be tabulated for each of the three classes of inflorescences. The results are given in Table VI.

Here the bimodal condition in the number of flowers per inflorescence found in the 1905 series does not appear, although the frequency of inflorescences with one flower is about as great as that of those with two. Doubtless the reason for this difference would be clear if we had as complete information concerning the 1905 series as is available for the 1909 material.

The purpose of the present note will have been fulfilled if in addition to the recording of a mass of definite quantitative data concerning the form of the inflorescence in Syndesmon, it convinces students of variation of the importance of a critical consideration of purely morphological features before concluding that an empirical multimodal polygon indicates the existence of biotypes.

COLD SPRING HARBOR, L. I.